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THE RÔLE OF SEDGES IN SOME COLORADO PLANT COMMUNITIES

FRANCIS RAMALEY

Every botanist is well aware of the large part taken by sedges in the vegetation of lake shores and swampy areas. For the eastern United States the species involved are well known, as also their relative importance in different stages of succession. Sedges of lake shores in the Rocky Mountains have been referred to by Clements (1), Ramaley and Robbins (7), Ramaley (4), and Robbins (9). In the present paper additional facts are given as to sedges of pondsides together with a series of observations on sedges of mesophytic and xerophytic habitats. This paper is based upon studies carried on largely from the University of Colorado Mountain Laboratory at Tolland, Colorado. Statements in the paper apply chiefly to the northern part of the state and to the mountain districts rather than to the plains. All species mentioned are well-known constituents of the Colorado flora. The nomenclature employed is that of Rydberg's "Flora of the Rocky Mountains and the Adjacent Plains" (New York, 1917). The various life zones are given the following names in accordance with customary usage: Plains, Foothill, Montane, Subalpine, Alpine (4).

Sedges exist chiefly in primitive communities or unstable situations. An area in a region that is climatically mesophytic becomes eventually either forest or grassland in which sedges have a very small place. So also, a climatically xerophytic area grows poor in sedges as the ultimate type of vegetation appears. Most sedges are aquatics or marsh plants or else they are xerophytes. Only a few are true mesophytes, and even these are likely to become crowded out by grasses and herbaceous dicotyledons in a meadow which has developed from marsh. Meadow or prairie of xerarch origin is also typically without sedges, the xerophytic sedges of more primitive stages disappearing before the meadow stage is reached. In the following systematic account the various genera of Cyperaceae are briefly considered, but chief attention is given to *Carex*.

SCIRPUS

Scirpus lacustris and other species of the genus are too well known everywhere to need description or comment. At lower elevations in Colorado, *i. e.*, on the plains, they behave very much as in the eastern part of the United States. They are found to some extent in the foothill area but are typically absent from lakes of the montane and higher zones.

ELEOCHARIS

Eleocharis acicularis, a small tufted spike-rush, is to be found somewhere along the shore of almost every lake or pond in the plains, foothill, and montane regions of Colorado. It does not grow on a coarse-grained substratum, but becomes established in fine sand, in clay, or in loam. Being firmly fixed by rhizomes and fibrous roots and producing a dense matted growth, it is a good soil binder against wave action. In Boulder Park, at Tolland, Colorado, as shown by Robbins (9), *Eleocharis acicularis* is associated with *Ranunculus reptans* in forming the characteristic pioneer community of mud flats along streams.

Eleocharis palustris, a much larger species, grows more in the water and often in almost pure stand, effectively filling up shallow pools in a few years. Both spike-rushes occur all the way from the plains to subalpine stations. A great many montane and subalpine lakes are, however, entirely free from *Eleocharis lacustris*. Its place is sometimes taken, ecologically, by *Sparganium angustifolium*. Other species of *Eleocharis* occur in the area studied, but the writer has slight acquaintance with them.

CYPERUS

Although five species of *Cyperus* are reported from Colorado, not any of them are conspicuous or important. They are confined to the plains region where they occur along streams and at margins of lakes or reservoirs, usually in wet, sandy soil. The commonest species is *Cyperus inflexus*, a rather diminutive annual confined to sandy shores recently exposed by lowering of a lake level or shifting of a stream bed. Such habitats are likely to be occupied soon, if not in the first place, by *Agrostis hiemalis*, *Eleocharis acicularis*, or *Alopecurus aristulatus*.

ERIOPHORUM

The species of *Eriophorum*, three in Colorado, are confined to habitats where the substratum is of a peaty nature. The writer has seen them only as very minor members in the Montane-Subalpine Sedge Moor Association.

DULICHIMUM, FIMBRYSTILIS, ELYNA

These genera, represented in Colorado by one, two, and one species respectively, are of rare or unusual occurrence. The writer has made no observations of interest upon them.

CAREX

Carex is well represented in northern Colorado. Unlike other genera of Cyperaceae which are practically all marsh plants, there are many species of *Carex* in mesophytic and xerophytic situations. In the following ac-

count the various association types in which Carices are important, together with the associations which belong to them, are briefly indicated. The categories, *association*, *association type*, *society*, *climatic climax association*; etc., are employed as defined by Nichols (3).

LIST OF PLANT COMMUNITIES IN WHICH THE RÔLE OF CAREX IS
CONSIDERED

1. Half-submersed Carex Association Type (Inceptive Sedge Moor).
 - (a) Half-submersed Carex Association of moderate altitudes.
 - (b) Subalpine Half-submersed Carex Association.
2. Sedge Moor Association Type.
 - (a) Plains-Foothill Sedge Moor Association.
 - (b) Montane-Subalpine Sedge Moor Association.
 - (c) Alpine Sedge Moor Association.
 - (d) Snow Patch Sedge Association.
3. Meadow Association Type.
 - (a) Plains-Foothill Streambank Meadow Association.
 - (b) Prairie Grass Association (of mesas and foothills).
 - (c) Montane Meadow Association.
 - (d) Subalpine Meadow Association.
 - (e) Alpine Meadow Association.
4. Xerophytic Carex Grassland Association Type.
 - (a) *Carex stenophylla* Grassland Association.
 - (b) *Carex rossii* Grassland Association.
 - (c) *Carex siccata* Grassland Association.
 - (d) *Carex elynoides* Grassland Association.

Half-submersed Carex Association Type (Inceptive Sedge Moor).

A number of species of *Carex* occur commonly in water at the margins of ponds or lakes or meandering streams. In such situations they are pioneer soil formers, as they lessen wind and wave action and favor the accumulation of humus. These same species often occur in sedge moor and will therefore be listed also in the account of that association type.

(a) *The Half-submersed Carex Association of moderate altitudes.*—Here the species are chiefly *Carex rostrata*, *C. lanuginosa*, *C. vesicaria*, *C. canescens*. In addition to these, almost any of the sedge-moor Carices may be found locally in standing water. In montane lakes *C. rostrata* is the commonest species.

(b) *The Subalpine Half-submersed Carex Association* consists chiefly of *C. aquatilis*. Except in lakes that are already considerably insilted, it does not form a complete circum-area but occurs near the inlet or outlet.

There is no half-submersed zone in alpine lakes. This is due partly to the fact that they are geologically young, the lake bottom being made of

large broken rocks with no soil. Another reason is that these lakes are frozen over from November to June, or as late as July. Even during August, the water temperature as shown by Dodds (2) is low, about 10 degrees Centigrade. Wherever the vegetation comes close to the edge of the water it is a dense growth of mosses and sedges, *i. e.*, a *moss moor*. This

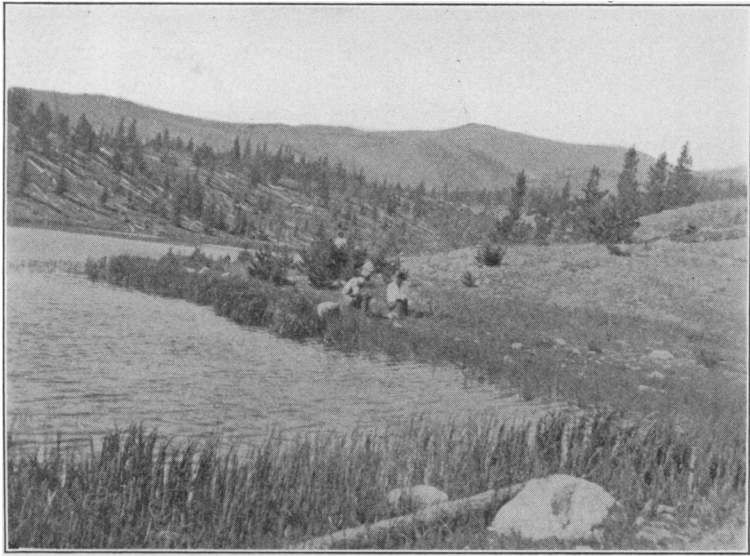


FIG. 1. A high montane lake (Teller Lake) showing Half-submersed Carex Association of *Carex rostrata* and *Carex canescens*. This is followed by a narrow zone of Sedge Moor dominated by *Carex aquatilis*. Outside of this is a strip of Meadow in which *Carex festivella* is important; farther out is a mixed Dry Grassland with a large amount of *Carex siccata*.

is usually elevated as a distinct "rim" one or two decimeters higher than the sedge moor, just as pointed out for montane lakes by Robbins (9). *Carex scopulorum* is probably the commonest sedge of the "rim."

Sedge Moor Association Type

This type of plant community exists under conditions similar to that described in the preceding section, but the soil is not covered by water. Ponds and lakes occur abundantly in the montane, subalpine, and alpine zones, and they always have some bordering sedge moor. The lakes at higher elevations are either morainic or of the rock-basin type. In the montane parks meandering streams give rise to ox-bows. The foothill area with its older topography and better drainage has very few lakes. A considerable number of natural lakes exist on the plains. Some of these are of ox-bow origin, some occupy old channels closed by alluvial damming, and some basins have arisen through wind action upon weathered sand-

stone or shale. All of these various bodies of water afford stations for sedges. The many artificial reservoirs for irrigation show a scant shore vegetation because of the frequent great changes in water level.

The term *sedge moor* as used by the present writer is meant to include all communities in wet soil dominated by Carices and often having a considerable amount of moss.¹ In some places it dries out to a degree in late August, but is saturated or nearly saturated during most of the growing season. According to Robbins (9), the soil water has a slightly acid reaction.

Sedge moor is an early stage in the hydrarch sequence. As the soil becomes built up through peat formation, or as the related stream or lake is lowered so that the water table sinks farther below the surface, a willow thicket develops or else a wet meadow. If it is the willow thicket that is produced, it will, in turn, be followed by meadow, and this again, in mountain districts, may be replaced by coniferous forest.

In Colorado, as pointed out by Robbins (9), Sphagnum bog does not occur. The nearest approach to it is sedge moor. It is true that Sphagnum moss is found locally in montane and subalpine situations, but it is not abundant. Most of the characteristic plants of bogs of the eastern United States are not present in Colorado at all; a few exist in isolated localities.

In all sedge moors Carices cover from 60 to 90 percent of the soil surface. Mosses are abundant, and liverworts (*Marchantia*) also, except at the higher elevations. Grasses are generally present, differing in species with the life zone; and a number of dicotyledons occur, chiefly of the Polygonaceae, Alsinaceae, Ranunculaceae, Gentianaceae, Scrophulariaceae, Carduaceae, and Cichoriaceae. As would be expected from likeness of edaphic conditions, there is considerable floristic similarity in sedge moors, even between those rather widely separated in altitude.

Three sedge moor associations may be recognized in northern Colorado, named in accordance with the life zones in which they commonly occur. The species, so far as known to the present writer, are listed for each association,—roughly in order of importance.

(a) *Plains-Foothill Sedge Moor Association*: *Carex lanuginosa*, *C. nebraskensis*, *C. aquatilis*, *C. rostrata*, *C. canescens*, *C. stipata*, *C. lasiocarpa*, *C. vesicaria*, *C. tenuirostris*.

(b) *Montane-Subalpine Sedge Moor Association*: *Carex aquatilis* (characteristic).—There are two societies. The *Montane Society* has the following secondary species: *Carex rostrata*, *C. vesicaria*, *C. lanuginosa*, *C. canescens*, *C. halleri*, *C. illota*, *C. lasiocarpa*, *C. tenuirostris*, *C. disperma*, *C.*

¹ Along streams the proportion of moss is often very high and the association becomes so modified as to be more properly designated as *moss moor*. The same term may be applied to that part of the moor of certain lakes which is closest to the water. High-altitude lakes show often other types of moor also, viz.: a *meadow moor* and a *heath moor*.

aurea, *C. paupercula*. In the *Subalpine Society* there are subsidiary species as follows: *Carex scopulorum*, *C. nigricans*, *C. paupercula*, *C. phaeocephala*, *C. illota*, *C. albonigra*.

(c) *Alpine Sedge Moor Association*: *Carex scopulorum*, *C. nigricans*, *C. nelsonii*, *C. chalciolepis*, *C. capillaris*.—*Carex scopulorum* and *C. nigricans* are common around springs and in seepage areas everywhere near the top of the Continental Divide.

(d) *Snow-Patch Sedge Association*.—In the subalpine and alpine zones snow drifts often remain on the ground until midsummer. In such places, if there is some accumulation of fine-grained soil, *Carex nigricans* is likely to form an almost pure stand. The snow accumulates year after year at the same point, and the very short period each year in which the ground is free from snow does not permit the establishment of many plant species. A typical area of snow-patch sedge association is made up almost wholly of *Carex nigricans*. A few subordinate species are represented by scattered individuals in very small amount. These are *Carex scopulorum*, *Ranunculus adoneus*, *Sibbaldia procumbens*, *Caltha rotundifolia*, *Trollius albiflorus*, *Polytrichum* and other mosses. The general appearance is quite different from that of ordinary sedge moor because of the low stature and broad leaves, widely spreading, of the dominant species. The snow-patch sedge association is interesting as being a rather primitive community and at the same time an ultimate one. The edaphic conditions are such that no successional stage can develop, at least so long as the mountains stand and snow continues to fall and to drift each winter.

Meadow Association Type

Meadow, as here understood, comprises all mesophytic grassland, but does not include anything that could be called sedge moor or marsh. Meadow grassland at lower altitudes in Colorado occurs in rather small strips where edaphic conditions are favorable to its development. The plains and foothill regions are too dry to support meadow on level ground or on south-facing slopes. Alluvial fans of fine-grained black soil support a mesophytic grassland designated by Vestal (10) as the Western Mesophytic Prairie Grass Association. Fringes of meadow occur along water courses, especially at bends of streams, and also next to (*i.e.*, in drier soil than) the sedge moor or willow thicket of mountain lakes. Hillside meadows, sometimes of considerable extent, occur in the montane zone. The higher rainfall and lower temperature of the subalpine and alpine zones are suitable for meadow development, and the association is often well developed. Lack of humus in the soil is, however, a limiting factor of importance.

A number of species of *Carex* occur in meadows, but only a few are abundant. The most important one is *Carex festivella*. It extends through

foothill, montane, and subalpine zones and to the lower part of the alpine. In the montane zone, where it is most abundant, it is associated with the plants named later as characteristic of the Montane Meadow Association. *Carex ebenea* has much the same distribution. These species sometimes dominate rather definite societies. As the soil becomes better drained the Carices are likely to be crowded out by grasses and dicotyledons. They are to be considered then as belonging to edaphic rather than to climatic meadows.

Carices of meadows and other mesophytic situations in addition to those thus far mentioned are all of less importance. The following are known to the writer: *Carex praegracilis*, *C. pachystachys*, *C. praticola* of moderate elevations, and *C. albonigra*, *C. bella*, *C. illota*, and *C. nova* in the subalpine and alpine zones. *C. chalciolepis* occurs in moist parts of alpine meadow. *C. douglassii* is a dry grassland species which is found to some extent in foothill meadow, while *C. siccata*, a species of dry hillsides and forest openings, is sometimes locally frequent in meadows of the montane zone.

The more typical meadows of northern Colorado may be distinguished as follows:

(a) *Plains-Foothill Streambank Meadow Association*, originally dominated by *Poa pratensis* but now much modified by the presence of *Trifolium repens* and *Phleum pratense*. This type of meadow is commonly without *Carex*.

(b) *Prairie Grass Association*, of Vestal (10, 11), belonging to lower alluvial slopes of mesas and foothills. Carices are of slight importance. *Carex heliophila* may be locally abundant in drier parts which have not yet reached the true meadow stage. In moister situations, especially where the soil has been recently carried in and the meadow is still in an inceptive stage, *Carex festivella*, *C. praegracilis*, and others may be present; their stay is quite temporary.

(c) *Montane Meadow Association*, of streambanks and pondsides, highly variable in floristic composition and with many consociations and societies as shown by Reed (8); often including *Potentilla pulcherrima*, *Erigeron macranthus*, *Fragaria glauca*, *Valeriana edulis*, *Pentstemon procerus*, *Tium alpinum*, *Pedicularis parryi*. Here there is often a considerable amount of *Carex*, especially *C. festivella* and *C. ebenea*.

(d) *Subalpine Meadow Association*, with such principal species as *Erigeron salsuginosus*, *Potentilla diversifolia*, *Antennaria umbrinella*, *Ligusticum tenuifolium*, *Castilleja lauta*, and *Castilleja rhexifolia*. In this association also the Carices are *C. festivella* and *C. ebenea*, with a sprinkling of various relicts of the former sedge moor stage.

(e) *Alpine Meadow Association*, with the following as some of the principal species: *Acomastylis turbinata*, *Bistorta bistortoides*, *Castilleja occidentalis*, *Trifolium dasyphyllum* and *Trifolium parryi*, *Rydbergia grandiflora*, *Campanula petiolata*. Associated Carices are quite frequent and may

be almost any of the species previously noted as belonging to high altitudes. Even some of the sedge-moor *Carices* may here enter the meadow, since the limits of plant associations in the alpine zone are not at all clearly marked.

Xerophytic Carex Grassland Association Type

Four xerophytic *Carices* are especially important as being the dominant species of definite associations, often covering areas of considerable extent. These associations will be considered in order, beginning at the lower altitudes.

(a) *Carex stenophylla* Grassland Association.—This is a highly primitive association, well developed in open parks of the foothill and montane zones

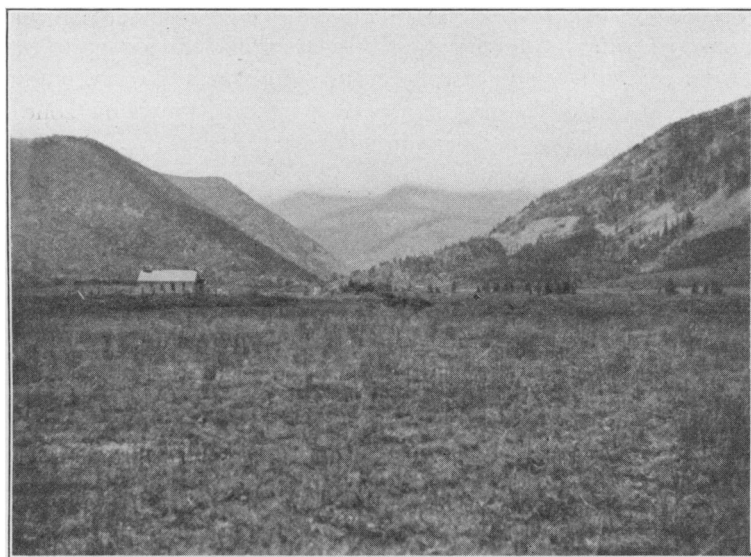


FIG. 2. *Carex stenophylla* Association on an old flood plain at Tolland, Colorado. The *Carex* plants, scarcely a decimeter tall, form a thin sod. At this particular point very few plants of secondary species are present.

in coarse sandy and gravelly soil lacking in humus. Plants of *Carex stenophylla* are low, generally less than 1 dm. in height. They spread by means of rhizomes and produce a rather thin sod. In dry grassland of a mountain park at Tolland, Colorado (altitude 8,889 feet), as previously reported by the present writer (5), this association is well represented. Associated plants are such pioneers as *Selaginella densa*, *Erigeron trifidus*, *Potentilla concinna*, *Potentilla strigosa*. As soil conditions become more favorable through accumulation of humus the *Carex* becomes less important, its place being taken by such grasses as *Festuca*, *Agropyron*, *Koeleria*, *Danthonia*, and *Muhlenbergia*. The *Carex stenophylla* association is, then, the inceptive stage of typical xerophytic grassland dominated by true grasses.

(b) *Carex rossii* Grassland Association.—This community appears in clearings and burned areas of coniferous forest on exposed hillsides of the montane and subalpine zones. The plants of *Carex rossii* form dense mats from 1 dm. to 1 m. across, developing in sandy or gravelly soil especially on south and west exposures. Subordinate plants of the *Carex rossii* grassland are *Vaccinium caespitosum*, *Thermopsis divaricarpa*, *Chamaenerion spicatum*, *Carex siccata*, *Rubus melanolasius*, and various forest plants in small numbers. There are some lichens on the ground, especially species of *Cladonia* and *Peltigera* under stones or old logs. This association may give way soon to coniferous forest, since seedlings of *Pinus flexilis* and *Pinus murrayana* are likely to develop. When the new forest is well started the *Carex* has all but disappeared, it being intolerant of shade. In some situations, however, the reproduction of pines is poor, and it may be many decades or even centuries before the *Carex* grassland gives way to forest.

(c) *Carex siccata* Grassland Association.—This and the preceding community might be classed by some students as consociations, but to the writer they seem so different as to demand associational standing. *Carex siccata* spreads by rhizomes and forms a loose sod; it does not produce dense mats at all. *Carex siccata* is more likely to appear at higher altitudes. It is more tolerant of shade and less xerophytic than *C. rossii*. The associated plants with *C. siccata* are those already mentioned for the *C. rossii* grassland with some additions such as *Tessaranthium stenopetalum*, *Koeleria gracilis*, *Amarella plebeja*, *Sambucus* (scattered), etc. The *Carex siccata* grassland is often a temporary climax having a long period of existence. Frequently occurring near timberline where the establishment of tree seedlings is difficult at best, the *Carex* occupies the soil and may maintain itself for centuries without invasion.

(d) *Carex elynoides* Grassland Association.—This community is found on mountain tops and slopes in the alpine zone or occasionally at lower elevations. Unlike the two associations just named, this one does not develop so often on steep slopes with poor soil but on more nearly level ground where humus may accumulate. It is not, however, to be considered as mesophytic, differing markedly as it does from the hydrarch alpine meadow. Soil is drier and the vegetation cover is not so close. *Carex elynoides* is a densely caespitose species and will be best understood if described as the alpine form of *C. filifolia*. It occupies from 40 to 80 percent of the soil surface. Associated plants are partly xerophytes, as *Selaginella densa*, *Silene acaulis*, *Oreoxis alpina*, *Festuca minutiflora*, and *Tetranneuris lanigera*, and partly mesophytes, as *Trifolium dasyphyllum*, *Acomastylis turbinata*, *Rydbergia grandiflora*, and *Castilleja occidentalis*. This mingling of xerophytic and mesophytic forms is common everywhere in high altitudes because of the great diversity of soil depth and soil moisture in even a small area, presence of large rocks, and other disturbing factors. *Carex elynoides* grassland will probably become in time alpine meadow, but perhaps it will

be somewhat different from the present hydrarch meadow, the characters of which depend largely on local edaphic conditions. Just what the climatic alpine meadow will be toward which both the xerarch and hydrarch series necessarily tend is not now quite apparent. For a long time to come the *Carex elynoides* grassland will be found just where it now exists. It is of a more permanent character, because more mesophytic, than the communities dominated by *Carex stenophylla*, *C. rossii*, and *C. siccata*.

Carex in Various Xerophytic Associations

Less important xerophytic Carices may be listed without extended comment. *C. heliophila* (*pennsylvanica* of western authors) is frequent in the mixed grassland of mesas and foothills, extending occasionally to the montane zone. Other species found at moderate elevations, none of them of common occurrence, are *Carex brevior*, *C. occidentalis*, *C. xerantica*, *C. douglasii*. In the montane zone *Carex oreocharis* is somewhat abundant and *C. obtusata* rather occasional in dry grassland of parks; *C. geyeri* occurs in dry forest openings. At high altitudes *Carex phaeocephala* and *C. pyrenaica* are frequent species of dry rocky slopes. *C. perglobosa* is occasional on alpine ridges.

List of Species of Carex²

In the following list the species of *Carex* are arranged in three groups according to the "soil moisture index" employed by the writer (6). It need hardly be stated that species may sometimes be found outside their accustomed habitats.

(a) *Species in water or wet soil* (marsh plants), the soil moisture index 8, 9, or 10: *aquatilis*, *aurea*, *canescens*, *capillaris*, *chalciolepis*, *disperma*, *halleri*, *illota*, *lanuginosa*, *lasiocarpa*, *nebraskensis*, *nelsonii*, *nigricans*, *pauperula*, *phaeocephala*, *rostrata*, *scopulorum*, *stipata*, *tenuirostris*, *vesicaria*.

(b) *Species in meadow or other mesophytic situations*, the soil moisture index 6 to 7 or sometimes 5: *albonigra*, *bella*, *ebenea*, *festivella*, *illota*, *nova*, *pachystachya*, *praegracilis*, *praticola*.

(c) *Species in xerophytic situations*, the soil moisture index typically 4 but varying to 5 or 3: *brevior*, *douglasii*, *elynoides*, *geyeri*, *heliophila*, *obtusata*, *occidentalis*, *oreocharis*, *perglobosa*, *phaeocephala*, *pyrenaica*, *rossii*, *siccata*, *stenophylla*, *xerantica*.

SUMMARY

The foregoing paper deals with the part played by sedges in the plant communities of northern Colorado. It is based upon studies in all the life

² This is not a complete list of the Carices of northern Colorado but includes only the species mentioned in this paper. Most of the author's collections were originally identified by Dr. Theodor Holm, but recently the specimens have been gone over again by Kenneth K. Mackenzie, Esq. Thanks are due to both these gentlemen for their courtesy and painstaking care.

zones from plains to alpine heights. The various genera of Cyperaceae are considered in order, but chief attention is given to *Carex*. Brief statement is made of the association types in which Carices are prominent. The several associations belonging to these types are characterized as to ecological relations and floristic composition. Some of the subject headings are: Half Submersed *Carex* Association Type, Sedge Moor Association Type, Snow-Patch Association, Meadow Association Type, Xerophytic *Carex* Grassland Association Type.

It is pointed out that most sedges belong to early stages of succession in the vegetation of a region, some being prominent in the hydrarch and some in the xerarch sequence. As mesophytism is approached from either direction other species may become prominent for a time, but these are displaced by grasses and dicotyledons in the ultimate climatic association.

A list is given of 44 species of *Carex*, of which 20 are classed as water and marsh plants, 9 as species of meadow or other mesophytic situation, 15 as species of xerophytic habitats.

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